1871
ИнБЮМ – IBSS

Морской биологический журнал
Marine Biological Journal
2023, vol. 8, no. 2, pp. 3–17
https://marine-biology.ru

SCIENTIFIC COMMUNICATIONS

UDC 591.524.12-045.52(262.5)

SPATIAL-TEMPORAL DYNAMICS OF THE ZOOPLANKTON ASSEMBLAGE STRUCTURE IN COASTAL WATERS NEAR SEVASTOPOL IN THE SPRING–AUTUMN PERIOD

© 2023 **E. A. Galagovets and I. Yu. Prusova**

A. O. Kovalevsky Institute of Biology of the Southern Seas of RAS, Sevastopol, Russian Federation
E-mail: *didobe@mail.ru*

Received by the Editor 16.12.2020; after reviewing 01.04.2021;
accepted for publication 16.02.2023; published online 31.05.2023.

Zooplankton of the coastal water area near Sevastopol are quite well studied. However, there are few comprehensive investigations of local zooplankton assemblages involving the characterization of all the taxa forming them. Moreover, previous research was mainly based on material sampled in the Sevastopol Bay at only one or two stations – at the bay mouth and/or in its apex, and there was no analysis of zooplankton spatial variability within the bay. The aim of this work is to characterize the spatial-temporal dynamics of zooplankton communities in the Sevastopol Bay and the adjacent open coastal waters in the spring–autumn 2013. We analyzed zooplankton sampled in April–November 2013 in the western, central, and eastern Sevastopol Bay, as well as at three stations in the adjacent open coastal area: two miles from the Sevastopol Bay mouth, near the Uchkuevka village, and at the Kruglaya Bay mouth. To assess spatial-temporal differences in the taxonomic structure of zooplankton assemblages, we applied analysis of similarities (ANOSIM), used nonparametric multidimensional scaling (MDS), and determined the contribution of individual taxa to the Bray–Curtis dissimilarity between sample groups (SIMPER). When analyzing beta diversity, the Shannon index was applied. As revealed, during the study period, there were spatial-temporal differences in the abundance and taxonomic structure of zooplankton communities between various areas of the Sevastopol Bay and the adjacent open coastal waters. The highest degree of dissimilarity in the taxonomic structure of zooplankton was recorded between the central–eastern bay and the open coastal area. When comparing assemblages of these water areas, *R* values (ANOSIM) were 0.926, 0.572, and 0.761 ($p < 0.03$) in spring, summer, and autumn, respectively. The mean total abundance of zooplankton in the bay in all seasons was higher than in the open coastal water area: (5.3 ± 1.9), (16.3 ± 2.7), and (8.3 ± 1.4) thousand ind.·m^{-3} *vs.* (0.8 ± 0.3), (4.6 ± 1.2), and (3.4 ± 1.3) thousand ind.·m^{-3} in spring, summer, and autumn, respectively (mean ± *SE*; $p < 0.006$). There was a tendency towards higher density values in the central Sevastopol Bay. A change in the level of diversity and, accordingly, in the degree of complexity of zooplankton assemblage was revealed in the spatial-temporal aspect. In spring, the lowest level of diversity was registered, with a mean (± *SE*) value of the Shannon index *H’* of 1.09 ± 0.16. In summer and autumn, the values increased to 1.94 ± 0.11 and 1.48 ± 0.09, respectively. In summer–autumn period, the values of *H’* were higher in the open coastal area (2.07 ± 0.09) and lower in the inner water area (1.53 ± 0.09). As determined, the differences in the taxonomic structure between the communities of the compared water areas were driven by three dominant taxa in spring, nine in summer, and five in autumn.

Keywords: zooplankton, copepods, taxonomic structure, diversity, Sevastopol Bay

Zooplankton of the coastal water area near Sevastopol are quite well studied. Specifically, the dynamics of abundance and biomass of fodder zooplankton before and after the invasion of ctenophores *Mnemiopsis leidyi* A. Agassiz, 1865 and *Beroe ovata* Bruguière, 1789 is investigated [Datsyk et al., 2012; Hubareva et al., 2004], and long-term alterations in the Copepoda taxocene structure in 1976–1996 are described [Gubanova et al., 2002]. Much attention is given to the analysis of ecology of individual taxa, in particular, invasive species, and their effect on the structure of the zooplankton assemblage [Altukhov, Gubanova, 2006; Gubanova, 2000, 2003; Gubanova et al., 2016, 2019, 2020; Seregin, Popova, 2016]. Comprehensive studies of zooplankton communities in coastal waters near Sevastopol, including the characteristics of all the taxa that form them, are not so numerous; those were carried out mainly using material from the Sevastopol Bay and an external water area in the 1980s [Belyaeva, Zagorodnyaya, 1988; Kovalev, 1980] and early 2000s [Datsyk et al., 2012; Gubanova, 2003; Temnykh et al., 2008; Zagorodnyaya et al., 2007]. Previous investigations were based mostly on material sampled at one or two stations – at the bay mouth and/or in its apex (eastern area), while the analysis of the spatial variability of zooplankton within the bay was not carried out. However, ecological conditions in the bay are heterogeneous: the western area is characterized by a more intensive water exchange with the open sea; the eastern area is replenished with freshwater from the Chernaya River; and the central area is affected by a large amount of wastewater, both storm water runoff and industrial and household sewage [Gubanov et al., 2015; Pavlova et al., 1999]. This is bound to affect the state of assemblages in these water areas.

The aim of this study is to characterize the spatial-temporal dynamics of zooplankton communities in the Sevastopol Bay and adjacent open water areas in the spring–autumn 2013.

MATERIAL AND METHODS

The studies covered the coastal areas of Sevastopol (Fig. 1) – the Sevastopol Bay (sta. 1–7) and three stations in the open coastal waters: the areas two miles from the bay mouth (sta. M), near the Uchkuevka village (sta. U), and at the Kruglaya Bay mouth (sta. K). The works were carried out from April to November 2013 (Table 1). Zooplankton were sampled using a 0.1-m^2 Juday net fitted with 132-µm mesh. Vertical net hauls were taken at all stations in the first half of the day in the 10–0-m layer. The sea surface temperature was measured at the time of sampling. The samples were preserved in 4% solution of buffered formalin. The organisms were identified and measured under MBS-9 microscope at 10–140-fold magnification. Mass species were counted using a Bogorov chamber in 1/20 or 1/10 of the initial sample taken with 1-mL and 5-mL Stempel pipettes in several replicates, depending on the abundance of planktonic organisms in a sample. To count rare taxa, the entire sample volume was examined. Adult and juvenile copepods (including naupliar stages) were identified down to the species level; other animals were identified down to the genus, family, or order level (whenever possible). A total of 45 samples were analyzed.

Graphical and statistical analysis was performed using PRIMER v5.2.4 and SigmaPlot 12.5 software packages. Spatial-temporal variations in the taxonomic structure of zooplankton assemblages were assessed based on the algorithm for comparing the degree of variability of rank similarities (the statistic *R*) in the ANOSIM program applying the Bray–Curtis similarity index *S* (S = 100%, if compared samples are completely similar; $S = 0$, if compared samples are completely dissimilar [Clarke, Warwick, 2001]). The test statistic *R* characterizes observed dissimilarities in the structure of communities *between* sampling areas compared with dissimilarities between samples *within* each area. *R* value varies from −1 to 1. $R = 1$, if *all* replicates at the sampling site are more similar to each other than to *any* sample from another area. *R* value is close to zero, if the similarity between samples within and between water areas on average is the same [Clarke, Warwick, 2001]. To analyze beta diversity, the Shannon index *H'* (log *e*) was applied. When ordinating by the method of nonparametric multidimensional scaling (MDS), the Bray–Curtis indices were used with 10 permutations for determining the lowest value of the stress index. When performing the procedures of cluster analysis, MDS, and SIMPER (determining the contribution of individual taxa to similarity/dissimilarity between groups of samples), the Bray–Curtis similarity matrix was constructed based on the initial data transformed to the power of 0.5 [Clarke, Warwick, 2001]. When constructing a matrix for cluster and MDS analysis, the data for each season for each station (*inter alia* for conditional sta. B2 and B3) were preliminarily averaged. Differences between the mean values of the Shannon index were assessed using Student's *t*-test (ANOVA) for a significance level of $p = 0.05$, and between the mean abundance values, according to the Mann–Whitney rank test for a significance level of $p < 0.01$. To designate certain sites of the water area studied, the following abbreviations were used: B1, the western Sevastopol Bay (sta. 1); B2, the central bay (sta. 2–4); B3, the eastern bay (sta. 5–7); and MKU, the open coastal water area (sta. M, K, U).

Table 1. Sampling dates and areas, number of the samples analyzed

Season 2013	Sea surface temperature range, °C	Site, sampling depth					
		The Sevastopol Bay, 10–15 m			Two miles from the coast, 50 m	The Kruglaya Bay, 20 m	Uchkuevka, 50 m
		sta. 1	sta. 2–4	sta. 5–7	M	K	U
		B1	B2	B3	MKU	MKU	MKU
		Number of samples					
Spring (11.04–25.04)	+10.3…+11.9	2	2	1	1	1	2
Summer (11.07–19.09)*	+23.0…+25.4	5	2	3	3	3	3
Autumn (11.10–14.11)	+13.7…+15.5	4	6	3	1	–	3

Note: B1, the western Sevastopol Bay (sta. 1); B2, the central bay (sta. 2–4); B3, the eastern bay (sta. 5–7); MKU, the open coastal water area (sta. M, K, U). *, according to the classification of hydrological seasons in the neritic zone of the Black Sea proposed by V. Greze *et al.* [1971], the September data were referred to summer season data.

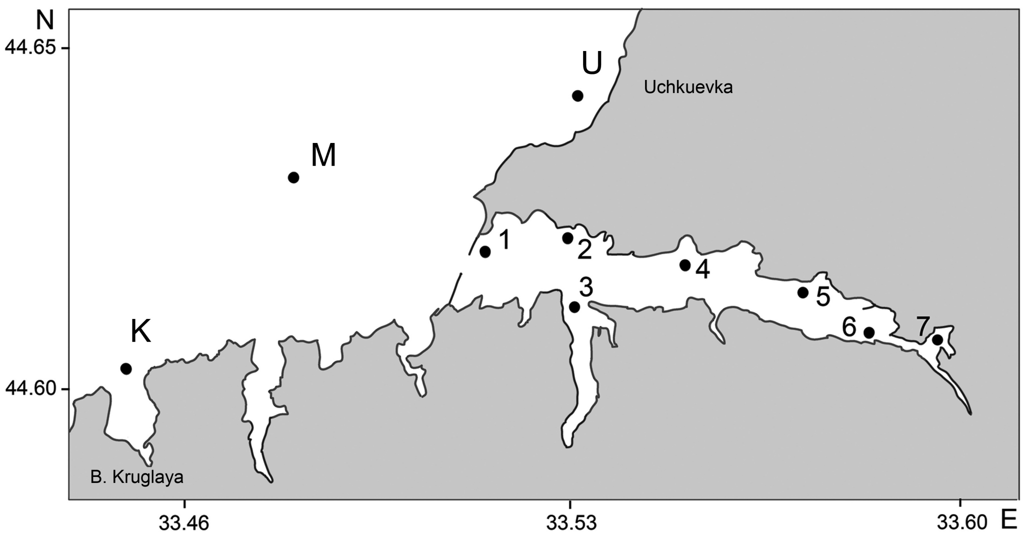

Fig. 1. The map of sampling stations: sta. K, the Kruglaya Bay mouth; sta. M, two miles from the Sevastopol Bay mouth; sta. U, near the Uchkuevka village; sta. 1–7, in the Sevastopol Bay

RESULTS AND DISCUSSION

Taxonomic composition and mean abundance of zooplankton. In analyzed material, 26 zooplankton taxa were recorded (Table 2); out of them, 16 were identified down to the species level. The cells of the flagellate *Noctiluca scintillans* were taken into account as well. Holoplankton was represented mainly by copepods, and their contribution to the total population was 25.5, 74.4, and 87.0% in spring, summer, and autumn, respectively (Table 3). A relatively small proportion of Copepoda in spring was due to high density of Rotifera in this season (see Table 3). Out of meroplankton organisms, the most abundant were larvae of Cirripedia, Polychaeta, and Mollusca (Bivalvia and Gastropoda), with the contribution to the total abundance of zooplankton within 2.5–10.1, 0.8–4.2, and 1.4–5.6%, respectively. The total mean abundance (excluding *N. scintillans*) was the highest in summer and the lowest in spring (Table 3).

Table 2. Taxonomic composition, mean abundance, and occurrence of zooplankton taxa in the studied water area in the spring–autumn 2013

Taxon	Mean abundance, ind.·m^{-3}	Standard error (*SE*), ind.·m^{-3}	Occurrence in samples, %	Season		
				Spring	Summer	Autumn
Copepoda						
Oithona davisae Ferrari & Orsi, 1984	3,488.2	831.7	91	+	+	+
Acartia clausi Giesbrecht, 1889	795.1	120.4	100	+	+	+
Acartia tonsa Dana, 1849	449.4	144.2	38	–	+	+
Paracalanus parvus (Claus, 1863)	379.9	68.7	91	+	+	+
Centropages ponticus Karavaev, 1895	205.2	44.6	82	+	+	+
Pseudocalanus elongatus (Boeck, 1865)	71.3	17.5	56	+	+	+
Oithona similis Claus, 1866	44.9	18.4	36	+	+	+
Calanus euxinus Hulsemann, 1991	36.7	9.8	60	+	+	+
Harpacticoida	13.2	5.0	49	+	+	+
Cyclopina gracilis Claus, 1863	0.5	0.4	4	+	+	–
Pontella mediterranea (Claus, 1863)	0.3	0.2	13	+	–	–
Other groups of zooplankton						
Rotifera	422.8	336.9	20	+	+	+
Penilia avirostris Dana, 1852	288.0	130.2	58	–	+	+
Cirripedia (nauplii)	283.0	61.8	91	+	+	+
Oikopleura dioica Fol, 1872	247.4	59.2	73	+	+	+
Bivalvia (larvae)	189.0	63.6	98	+	+	+
Polychaeta (larvae)	177.4	67.0	84	+	+	+
Gastropoda (larvae)	106.3	19.9	84	+	+	+
Evadne spinifera P. E. Müller, 1867	84.2	33.0	31	–	+	–
Hydrozoa (larvae)	55.5	35.1	29	–	+	+

Continue on the next page…

Taxon	Mean abundance, ind.·m^{-3}	Standard error (*SE*), ind.·m^{-3}	Occurrence in samples, %	Season		
				Spring	Summer	Autumn
Parasagitta setosa (J. Müller, 1847)	47.6	17.4	67	+	+	+
Pleopis polyphemoides (Leuckart, 1859)	31.1	14.9	38	–	+	+
Pseudevadne tergestina (Claus, 1877)	22.6	12.8	16	–	+	–
Decapoda (larvae)	14.5	4.9	53	–	+	+
Isopoda	10.8	3.8	44	–	+	+
Nematoda	4.1	3.3	16	+	+	+
Noctiluca scintillans (Macartney) Kofoid & Swezy, 1921	242.5	87.1	29	+	+	–

Table 3. Seasonal mean values of the absolute and relative abundance of different taxonomic groups of zooplankton in the spring–autumn 2013

Taxon	Mean abundance ± *SE*, ind.·m^{-3}			Proportion in the total abundance, %		
	Spring	Summer	Autumn	Spring	Summer	Autumn
Appendicularia	2 ± 1	241 ± 96	384 ± 104	0.1	2.3	5.6
Chaetognatha	0	91 ± 39	24 ± 9	0	0.9	0.4
Cirripedia	352 ± 159	262 ± 106	270 ± 82	10.1	2.5	3.9
Cladocera	0	985 ± 347	27 ± 7	0	9.3	0.4
Copepoda	896 ± 150	7,898 ± 1,976	6,044 ± 998	25.7	74.6	87.3
Hydrozoa	0	123 ± 81	10 ± 6	0	1.2	0.1
Decapoda	0	31 ± 11	4 ± 2	0	0.3	0.1
Isopoda	0	21 ± 8	5 ± 2	0	0.2	0.1
Mollusca	49 ± 18	590 ± 153	96 ± 21	1.4	5.6	1.4
Nematoda	1 ± 0.7	9 ± 8	1 ± 0.5	0.0	0.1	0.0
Polychaeta	146 ± 71	304 ± 151	52 ± 18	4.2	2.9	0.8
Rotifera	2,044 ± 1,646	30 ± 22	4 ± 3	58.6	0.3	0.1
In total (without *Noctiluca scintillans*)	3,491 ± 1,797	10,583 ± 2,467	6,922 ± 1,143	–	–	–
N. scintillans	974 ± 328	113 ± 58	0	–	–	–

Sample grouping. The degree of similarity of the sampling areas (and, accordingly, the composition of zooplankton assemblages in these water areas) was analyzed by the MDS ordination based on the data on the abundance of organisms in the samples (Fig. 2).

In all seasons, the stations within the bay (groups B2 and B3) and in the open coastal area (sta. M, K, U) were grouped separately within the ordination plane, which reflects a certain degree of dissimilarities in the taxonomic structure between zooplankton communities in the bay and in the open coastal waters. The assemblage at the station at the bay mouth (sta. B1) was similar in species composition to the communities both in the inner bay area and in the open coastal area, which resulted from the intermediate location of the sta. B1. In terms of the degree of similarity of the species composition, this station was grouped in spring and summer with the stations of the open coastal water area, and in autumn, with the stations of the bay (see Fig. 2).

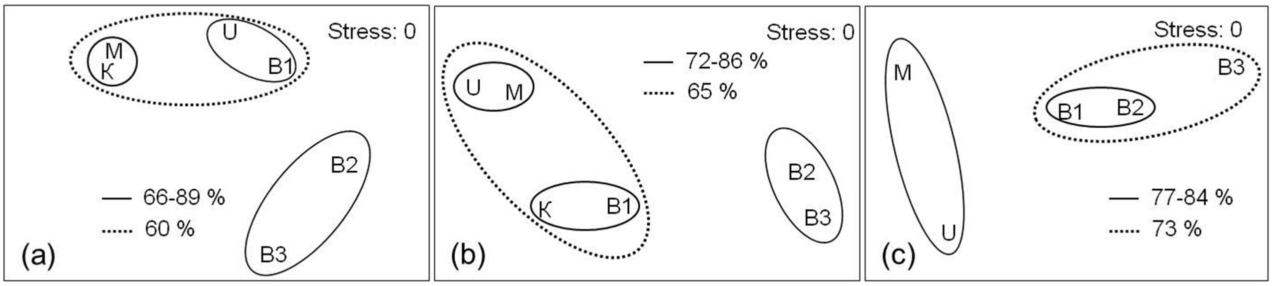

Fig. 2. Results of MDS ordination analysis; grouping of stations based on the taxonomic structure of zooplankton assemblages: a, spring; b, summer; c, autumn. Data on the abundance of zooplankton taxa averaged for each area were used. Solid and dashed lines correspond to the level (%) of grouping of areas (stations) by the results of cluster analysis

Taking into account the results of ordination, the degree of similarity between the identified groups of samples was analyzed (Table 4). The communities of the areas B2 and B3 were the most similar: the Bray–Curtis index *S* in the group B2 compared with the group B3 varied within 53–67%; in other compared groups, the value was lower in all seasons. The dissimilarities between the zooplankton assemblages in the bay waters and the open coastal area are confirmed by high values of the test statistic *R*, which assesses the degree of variability of average values of rank similarities for combinations of all pairs of stations from different groups compared with the variability of similarities between any pair of stations from the same group.

Table 4. Results of the test for spatial-temporal differences in the taxonomic structure of zooplankton assemblages when comparing groups of samples based on the abundance of taxa in the spring–autumn 2013

Areas under comparison	Spring			Summer			Autumn		
	S, %	*R*	*p*	*S*, %	*R*	*p*	*S*, %	*R*	*p*
B2 *vs.* B3	63.4	1.000	0.333	53.2	–0.083	0.400	67.5	0.243	0.143
B2 + B3 *vs.* MKU	35.9	0.926	**0.029**	42.6	0.572	**0.003**	47.2	0.761	**0.001**
B1 *vs.* B2 + B3	53.2	0.333	0.200	51.8	0.336	**0.008**	65.3	0.181	0.134
B1 *vs.* MKU	59.7	0.107	0.400	50.7	0.358	**0.011**	55.1	0.145	0.257
	Global *R*	*p*		Global *R*	*p*		Global *R*	*p*	
The entire water area studied	0.608	**0.022**		0.425	**0.001**		0.427	**0.005**	

Note: *S*, the Bray–Curtis similarity index; *R*, the test statistic (see "Material and Methods" section); *p*, the probability of acceptance of the hypothesis that there are no differences between the compared mean values ($p_0 = 0.05$). Statistically significantly different results are highlighted in bold.

For these areas, *R* values in spring, summer, and autumn were 0.926, 0.572, and 0.761, respectively; the dissimilarities between them were significant (Table 4). In the compared groups (B1 *vs.* B2 + B3; B1 *vs.* MKU), *R* values were low, from 0.107 to 0.358, indicating a low degree of dissimilarities within these groups. The generalizing value of *R* (global *R*), which characterizes the level of spatial differences between groups for each season as a whole, was significantly higher in spring than in summer and autumn (see Table 4). Global R values calculated for each of the areas – MKU, B1, B2, and B3 – were 0.790, 0.814, 0.992, and 0.556, respectively (at $p < 0.002$), and those were generally higher than the values of spatial variations.

The results obtained indicate that: 1) the taxonomic structure of zooplankton in the studied water areas is heterogeneous, and the degree of similarity between the communities of the central and eastern bay is higher than that for the western bay and the open coastal waters; 2) the highest degree of dissimilarity is recorded between the central–eastern bay and the open coastal area in all seasons; 3) spatial variability of zooplankton structure is higher in spring than in summer and autumn; and 4) seasonal variability of the structure is more pronounced than the spatial one.

Diversity index. Distinct seasonal differences in the values of the Shannon diversity index were registered for zooplankton assemblages of the open coastal water area (MKU): the mean value of H' in summer was significantly higher than in spring and autumn ($p < 0.001$) (Fig. 3). At the sta. B1 in summer, the value of H' was higher than in spring ($p = 0.016$); at the stations within the bay (sta. B2 + B3), seasonal differences in the mean values of H' were not revealed. For the entire water area studied, the mean value of H' in summer (1.94 ± 0.11) was significantly higher than in spring and autumn (1.09 ± 0.16 and 1.48 ± 0.09, respectively) ($p < 0.0041$).

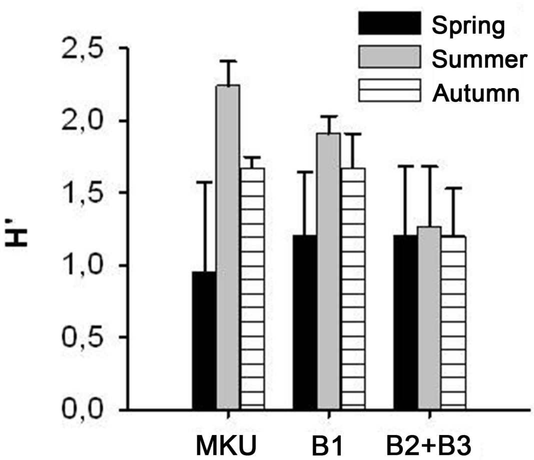

Fig. 3. Variability of mean values (mean ± *SE*) of the Shannon diversity index in the Sevastopol Bay (B1, B2 + B3) and the open coastal water area (MKU) in the spring–autumn 2013

The spatial dynamics of the Shannon diversity index values was as follows: in the summer–autumn period, the values of H' were higher in the open coastal area (2.07 ± 0.09) and lower in the water area within the bay (1.53 ± 0.09). In summer, the value of H' for each of three examined water areas (MKU, B1, and B2 + B3) differed significantly ($p < 0.001$), being the highest for the open coastal waters (2.26 ± 0.06) and the lowest for the area within the bay (1.66 ± 0.15). In autumn, at the stations within the bay (sta. B2 + B3), the value of H' (1.28 ± 0.11) was significantly lower than at the bay mouth (1.78 ± 0.15) and in the open coastal area (1.64 ± 0.04) ($p = 0.041$ and $p = 0.048$, respectively). In spring, the differences were insignificant.

Thus, lower values of the Shannon diversity index and, accordingly, lower taxonomic diversity of the community were revealed in spring throughout the entire water area. The degree of the assemblage complexity tended to increase towards the open coastal water area in summer and autumn. The stability of this trend is confirmed by the fact that a similar pattern of diversity variability in the bay water area was observed earlier on the material of 1981–1983, based on the analysis of spatial-temporal dynamics in the number of zooplankton species [Belyaeva, Zagorodnyaya, 1988].

Taxa determining dissimilarities between assemblages. Using the SIMPER procedure, discriminatory taxa were identified, the contribution of which to dissimilarities between the zooplankton communities of the open coastal area (sta. MKU), within the bay (sta. B2 + B3), and at the bay mouth (sta. B1) was the most significant and accounted for about 50% dissimilarities between the compared groups of samples (Table 5). In spring, the main contribution to the dissimilarity between groups of samples was made by 2–3 taxa prevailing in the assemblage; in autumn, there were more discriminatory taxa; and in summer, their number was maximum. The obtained results confirm the conclusions about the nature of prevalence and the degree of complexity of communities, which were made on the basis of the analysis of the spatial-temporal variability in the diversity index.

Table 5. Taxa with the largest contribution to the dissimilarity between zooplankton assemblages of different sites of the Sevastopol Bay and the open coastal water area in the spring–autumn 2013

Areas under comparison	Spring		Summer		Autumn	
	Taxon	Contribution to dissimilarity, %	Taxon	Contribution to dissimilarity, %	Taxon	Contribution to dissimilarity, %
B2 + B3 *vs.* MKU	Rotifera	34.0	*O. davisae*	25.5	*O. davisae*	28.2
	N. scintillans	21.4	*P. avirostris*	8.2	*A. clausi*	9.9
			A. tonsa	8.0	Cirripedia	9.5
			P. parvus	5.5	*P. parvus*	8.5
			O. dioica	5.4		
B1 *vs.* MKU	Cirripedia	20.6	*O. davisae*	18.2	*O. davisae*	16.0
	N. scintillans	19.0	*A. tonsa*	9.7	*A. clausi*	15.7
	Rotifera	10.3	Cirripedia	8.4	*O. dioica*	13.0
			C. ponticus	6.3	*P. parvus*	9.5
			O. dioica	5.1		
			Bivalvia	4.4		
B1 *vs.* B2 + B3	Rotifera	35.8	*O. davisae*	17.5	*O. davisae*	22.2
	N. scintillans	18.3	*A. tonsa*	8.3	*A. clausi*	12.2
			P. avirostris	7.5	*O. dioica*	9.7
			Cirripedia	6.7	Cirripedia	7.1
			P. parvus	6.4		
			C. ponticus	5.7		

Throughout the entire study period, the taxa determining dissimilarities between assemblages were five Copepoda species (*Acartia clausi*, *Acartia tonsa*, *Centropages ponticus*, *Oithona davisae*, and *Paracalanus parvus*), cladoceran *Penilia avirostris*, appendicularian *Oikopleura dioica*, Bivalvia and Cirripedia larvae, as well as rotifers and the flagellate *N. scintillans* (Table 5). These taxa had the highest values of the mean abundance (see Table 3). The composition of groups of discriminatory taxa in various seasons was different (Table 5), and this indicates seasonal differences in the structure of zooplankton communities (Fig. 4).

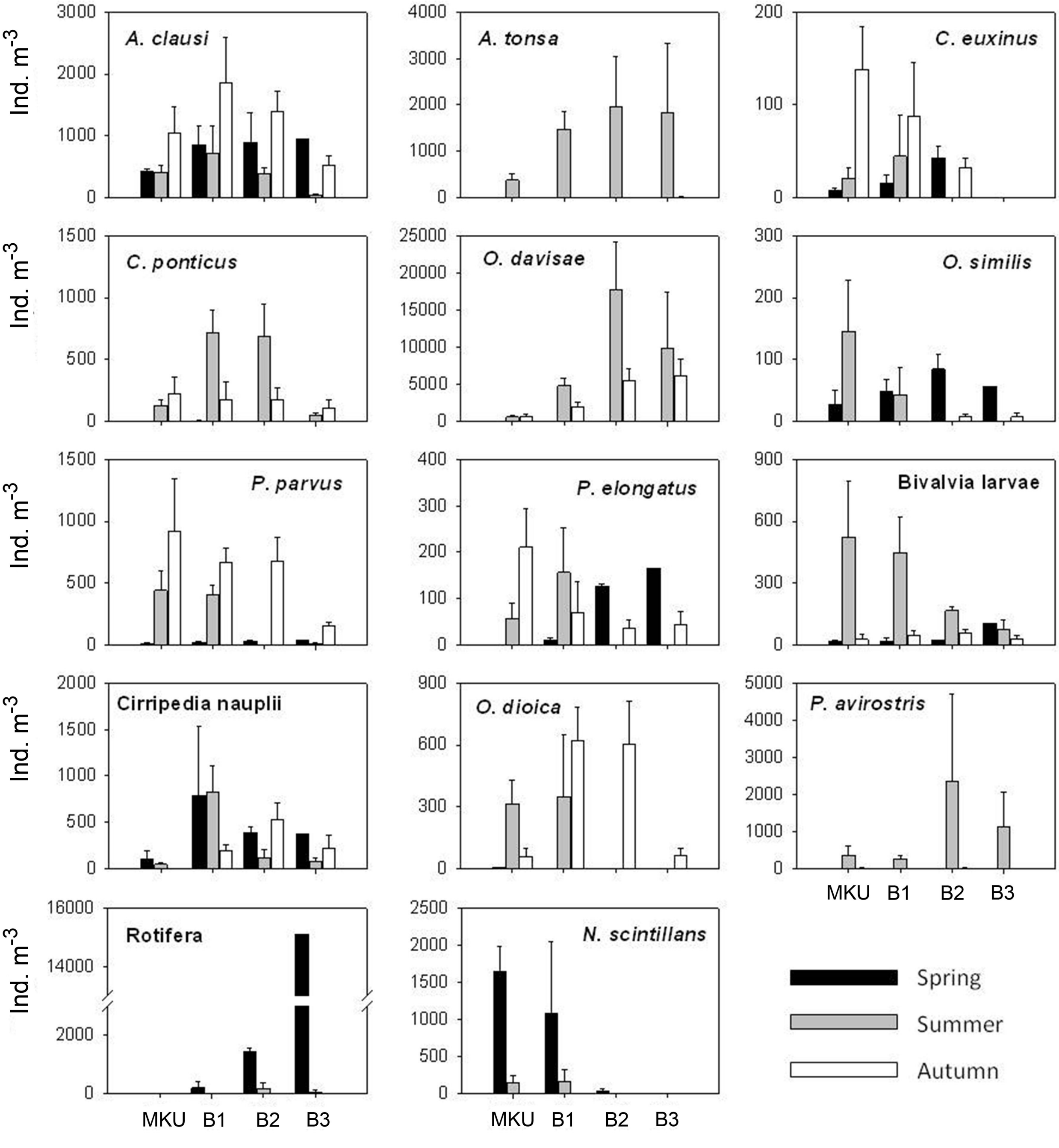

Fig. 4. Spatial-temporal dynamics of the mean abundance (mean ± *SE*) of the main Copepoda species and other most abundant taxa in the Sevastopol Bay (B1, B2, B3) and the open coastal water area (MKU) in the spring–autumn 2013

Dynamics of the zooplankton assemblage structure. In spring, Copepoda communities were distinctly dominated by *A. clausi* (74.8–89.3% of the total abundance of copepods in spring *vs.* 0.3–38.9% in summer and autumn), with almost complete absence of *C. ponticus* (0–0.4% in spring *vs.* 1.6–6.9% in summer) and a small contribution of other species (Fig. 5b). In summer–autumn, *O. davisae* prevailed (21.6–88.1% in summer and autumn *vs.* 0.3–4.8% in spring); it was the most common species in the studied material (Table 2), with the highest density values in summer (up to 24,950 ind.·m^{-3} in August at sta. 6). An important element in the assemblages of the summer period was *A. tonsa* (9.4–17.6% of the total Copepoda abundance), which was absent from plankton in spring and recorded as single individuals at two out of seven stations in autumn. *Calanus euxinus*, *Oithona similis*, and *Pseudocalanus elongatus* were present in plankton throughout the entire study period; their density was low (Fig. 4), and their contribution varied within 0.4–4.3, 0.1–7.1, and 0.1–13.1%, respectively. Therefore, the role of these species in the spatial-temporal dynamics of the zooplankton structure was insignificant.

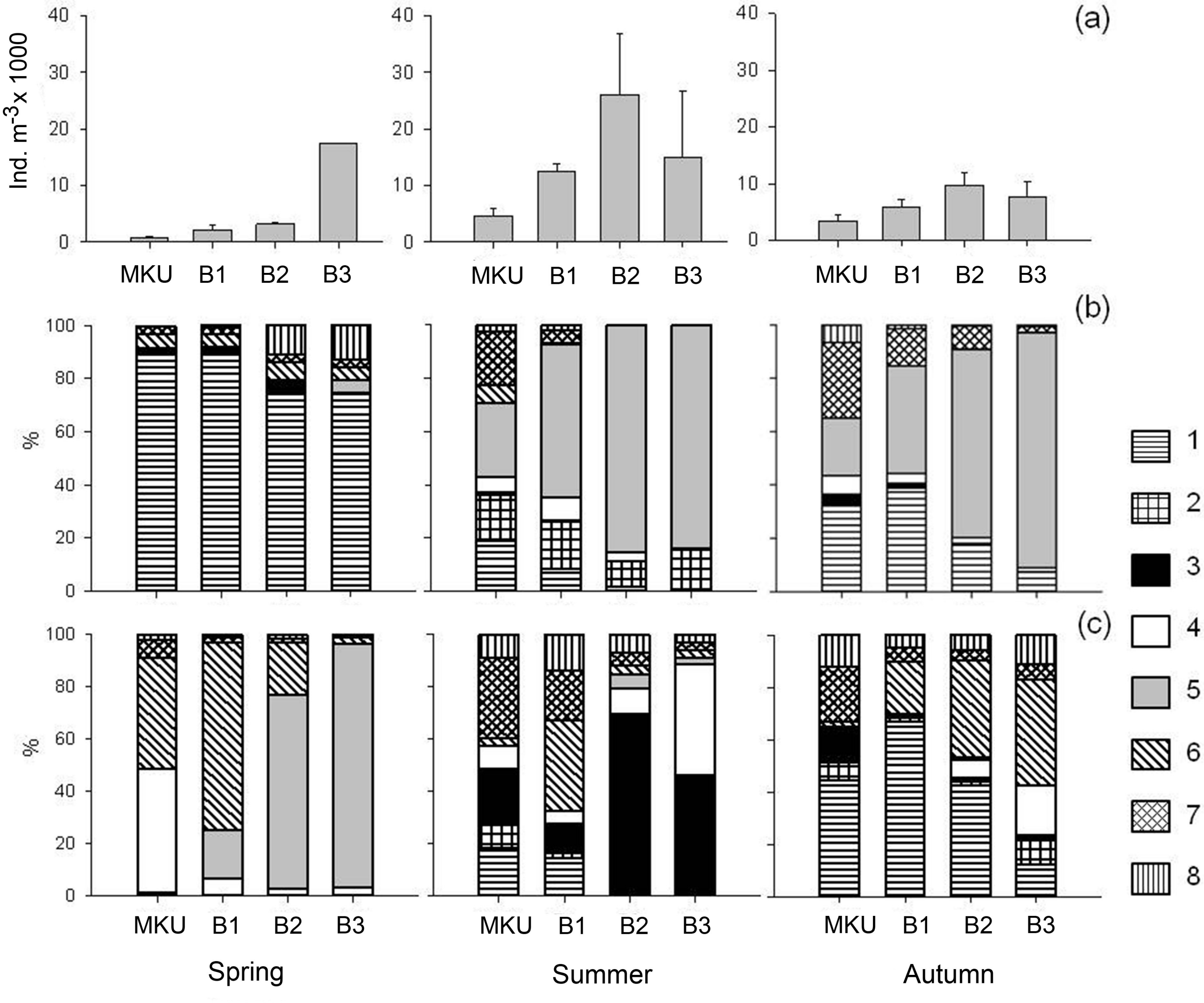

Fig. 5. Spatial-temporal dynamics of the total abundance (mean ± *SE*) of zooplankton (a) and taxonomic structure of Copepoda (b) and other taxa of forage zooplankton (c) in the Sevastopol Bay (B1, B2, B3) and the open coastal water area (MKU) in the spring–autumn 2013. For (b): 1, *Acartia clausi*; 2, *Acartia tonsa*; 3, *Calanus euxinus*; 4, *Centropages ponticus*; 5, *Oithona davisae*; 6, *Oithona similis*; 7, *Paracalanus parvus*; 8, *Pseudocalanus elongatus*. For (c): 1, *Oikopleura dioica*; 2, *Parasagitta setosa*; 3, *Penilia avirostris*; 4, Polychaeta larvae; 5, Rotatoria; 6, Cirripedia nauplii; 7, Bivalvia larvae; 8, Gastropoda larvae

Among the groups of other organisms, the largest range of seasonal density variations was found in Rotifera: from mean values of thousands of ind.·m^{-3} in spring to minimum values in summer and autumn (see Table 3). Rotifers were noted only in the bay water area (B1, B2, and B3) and not registered in the open coastal area. The spring peak of their abundance, 15,110 ind.·m^{-3}, was recorded in the area B3 (Fig. 4); it was 86.2% of the total abundance of zooplankton there. In spring, the communities differed significantly from those of summer ($p = 0.0034$) in higher population density of *N. scintillans*: (974 ± 328) ind.·m^{-3} *vs.* (113 ± 58) ind.·m^{-3} in summer. In autumn, this flagellate was absent in the plankton.

Spatial heterogeneity of the taxonomic structure of the Copepoda assemblage was determined mainly by the variability in the proportions of *A. clausi*, *A. tonsa*, *C. ponticus*, *O. davisae*, and *P. parvus*. In summer and autumn, the degree of spatial dissimilarity in the structure was more pronounced than in spring (Fig. 5b). In the group of other organisms, spatial variations in spring were mainly driven by the variability of the contribution of rotifers and Cirripedia larvae; in summer, *P. avirostris* and Polychaeta and Bivalvia larvae; and in autumn, *O. dioica* and Bivalvia larvae (Fig. 5c).

The mean abundance of total zooplankton in all seasons in the bay (B1 + B2 + B3) was significantly higher than in the open coastal area: (5.3 ± 1.9), (16.3 ± 2.7), and (8.3 ± 1.4) thousand ind.·m^{-3} *vs.* (0.8 ± 0.3), (4.6 ± 1.2), and (3.4 ± 1.3) thousand ind.·m^{-3} in spring, summer, and autumn, respectively (mean ± *SE*; $p < 0.006$). A similar ratio was registered separately for communities of copepods and other organisms, as well as for *A. tonsa* ($p = 0.0080$), *O. davisae* ($p = 0.0004$), and Cirripedia ($p = 0.0003$). The mean abundance of *A. clausi*, *C. ponticus*, *O. dioica*, and *P. avirostris* was also higher in the bay (Fig. 4), but the differences were not significant. The average population density of *C. euxinus*, *O. similis*, *P. parvus*, *P. elongatus*, *N. scintillans*, and Bivalvia larvae was slightly higher in the open coastal waters (Fig. 4), but the differences were not significant. Assessing the spatial variability of abundance values within the bay water area, it should be noted as follows. In summer and autumn, the total mean abundance of zooplankton in the central area (B2) was higher than in the eastern (B3) and western (B1) areas (Fig. 5a), but taking into account the variability values, these differences were not significant.

The revealed trend of increasing values of the assemblage abundance in the central Sevastopol Bay, compared to the values in its eastern and western areas, is consistent with previously reported results. Specifically, based on the material of 1981–1983, maximum zooplankton abundance and biomass were registered in the center of the bay [Belyaeva, Zagorodnyaya, 1988]. Spatial dissimilarities in zooplankton abundance values might be related to different environmental conditions in various bay areas, namely, to the level of eutrophication due to anthropogenic pollution. Based on the study of the distribution of phosphates, silicates, nitrates, nitrites, ammonium ions, and amount of suspended matter in the surface layer in 1998–2000, the western bay was assigned earlier to the areas with the level of weak pollution; the eastern bay, moderate pollution; and the central bay, heavy pollution [Lopukhin et al., 2007]. The central bay area may be characterized by a higher level of water trophicity, resulting in higher plankton abundance. In relatively clean waters of the open coastal area, lower zooplankton densities were recorded. Apparently, lower zooplankton density in the open coastal waters results from the fact that sampling was carried out only in the 10–0-m layer, but not in the entire inhabited water column.

Further studies in the waters of the Sevastopol Bay and open coastal areas, along with the analysis of hydrochemistry data, will supplement the obtained results and reveal the spatial patterns of the formation of zooplankton communities within this area.

Conclusion. Between various sites of the Sevastopol Bay area and the adjacent open coastal waters, spatial-temporal variability in the quantitative values and taxonomic structure of zooplankton assemblages was revealed in the spring–autumn 2013. In all seasons, the total mean zooplankton abundance in the bay was higher than in the open coastal water area. A tendency towards higher abundance values in the central bay was recorded. The highest level of variability in the zooplankton taxonomic structure was registered between the central–eastern bay and the open coastal waters. In the summer–autumn period, an increase in the diversity and, accordingly, in the level of community complexity from the eastern bay towards the open coastal area was noted. The lowest level of the assemblage diversity was observed in spring. As determined, the dissimilarities in the taxonomic structure between the communities of the compared water areas were due to three dominant taxa in spring, nine in summer, and five in autumn, including five Copepoda species (*Acartia clausi*, *Acartia tonsa*, *Centropages ponticus*, *Oithona davisae*, and *Paracalanus parvus*), cladoceran *Penilia avirostris*, appendicularian *Oikopleura dioica*, Bivalvia and Cirripedia larvae, rotifers, and the flagellate *Noctiluca scintillans*.

This work was carried out within the framework of IBSS state research assignment "Structural and functional organization, productivity, and sustainability of marine pelagic ecosystems" (No. 121040600178-6).

Acknowledgement. The authors are grateful to S. Ignatyev and D. Altukhov for their help in zooplankton sampling and to anonymous reviewers for their valuable comments.

REFERENCES

1. Altukhov D. A., Gubanova A. D. *Oithona brevicornis* Giesbrecht in the Sevastopol Bay in October, 2005 – March, 2006. *Morskoj ekologicheskij zhurnal*, 2006, vol. 5, no. 2, pp. 32. (in Russ.). https://repository.marine-research.ru/handle/299011/865
2. Belyaeva N. V., Zagorodnyaya Yu. A. Zooplankton of the Sevastopol Bay in 1981–1983. *Ekologiya morya*, 1988, iss. 29, pp. 77–84. (in Russ.). https://repository.marine-research.ru/handle/299011/3844
3. Greze V. N., Baldina E. P., Bileva O. K. Dinamika chislennosti i produktsii osnovnykh komponentov zooplanktona v neriticheskoi zone Chernogo morya. *Biologiya morya*, 1971, iss. 24, pp. 12–49. (in Russ.). https://repository.marine-research.ru/handle/299011/1592
4. Gubanov V. V., Gubanova A. D., Rodionova N. Yu. Diagnosis of water trophicity in the Sevastopol Bay and its offshore. In: *Current Issues in Aquaculture* : proceedings of the International Scientific Conference, Rostov-on-Don, 28 September – 02 October, 2015. Rostov-on-Don : FGBNU "AzNIIRKh", 2015, pp. 64–66. (in Russ.)
5. Gubanova A. D. *Acartia tonsa* Dana in the Sevastopol Bay: Appearance, seasonal dynamic, size structure. *Ekologiya morya*, 2000, iss. 51, pp. 55–58. (in Russ.). https://repository.marine-research.ru/handle/299011/4299
6. Gubanova A. D. Long-term changes in the specific composition and abundance of genera *Acartia* Dana copepod in the Sevastopol Bay. In: *Modern Condition of Biological Diversity in Near-shore Zone of Crimea (the Black Sea Sector)* / V. N. Eremeev, A. V. Gaevskaya (Eds) ; NAS Ukraine, Institute of Biology of the Southern Seas. Sevastopol :

EKOSI-Gidrofizika, 2003, pp. 94–104. (in Russ.). https://repository.marine-research.ru/handle/299011/1467

7. Gubanova A. D., Altukhov D. A., Popova E. V., Garbazey O. A. *Oithona davisae*, the new species of copepods in the Black Sea: Long-term dynamics, spatial distribution and impact on zooplankton community. In: *Morskie biologicheskie issledovaniya: dostizheniya i perspektivy* : v 3 t. : sb. materialov Vseros. nauch.-prakt. konf. s mezhdunar. uchastiem, priuroch. k 145-letiyu Sevastopol'skoi biologicheskoi stantsii, Sevastopol, 19–24 Sept., 2016. Sevastopol, 2016, vol. 1, pp. 154–157. (in Russ.)
8. Hubareva E. S., Svetlichny L. S., Romanova Z. A., Abolmasova G. I., Anninsky B. E., Finenko G. A., Bat L., Kideys A. Zooplankton community state in the Sevastopol Bay after the invasion of ctenophore *Beroe ovata* in the Black Sea (1999–2003). *Morskoj ekologicheskij zhurnal*, 2004, vol. 3, no. 1, pp. 39–46. (in Russ.). https://repository.marine-research.ru/handle/299011/732
9. Datsyk N. A., Romanova Z. A., Finenko G. A., Abolmasova G. I., Anninsky B. E. Zooplankton community structure in the inshore waters of the Crimean coasts (Sevastopol area) and trophic relations in the food chain zooplankton–*Mnemiopsis* in 2004–2008. *Morskoj ekologicheskij zhurnal*, 2012, vol. 11, no. 2, pp. 28–38. (in Russ.). https://repository.marine-research.ru/handle/299011/1210
10. Zagorodnyaya Yu. A., Temnykh A. V., Moryakova V. K. Holoplankton seasonal dynamics in inshore waters of the Black Sea in 2002. *Morskoj ekologicheskij zhurnal*, 2007, vol. 6, no. 1, pp. 31–43. (in Russ.). https://repository.marine-research.ru/handle/299011/894
11. Kovalev A. V. Sezonnye izmeneniya zooplanktona v Sevastopol'skoi bukhte. *Gidrobiologicheskii zhurnal*, 1980, vol. 16, no. 6, pp. 9–14. (in Russ.). https://repository.marine-research.ru/handle/299011/2866
12. Lopukhin A. S., Ovsyany E. I., Romanov A. S., Kovardakov S. A., Sysoeva I. V., Bryantseva Yu. V., Ryl'kova O. A., Gavrilova N. A., Gubanov V. V., Lopukhin S. A., Kamenir Yu. G., Gomis C., Wilson J. G., Kemp R. B. Seasonal peculiarities of hydrologic-hydrochemical structure of Sevastopol Bay water, microplankton and distribution of its biochemical components (the Black Sea, observations of 2004–2005). *Ekologicheskaya bezopasnost' pribrezhnoi i shel'fovoi zoni i kompleksnoe ispol'zovanie resursov shel'fa*, 2007, no. 15, pp. 74–109. (in Russ.)
13. Pavlova E. V., Ovsyany E. I., Gordina A. D., Romanov A. S., Kemp R. B. Modern state and tendencies of change in Sevastopol Bay ecosystem. In: *Akvatoriya i berega Sevastopolya: ekosistemnye protsessy i uslugi obshchestvu* / E. V. Pavlova, N. V. Shadrin (Eds). Sevastopol : Akvavita, 1999, chap. 2, pp. 70–95. (in Russ.). https://repository.marine-research.ru/handle/299011/5248
14. Seregin S. A., Popova E. V. Long-term dynamics of abundance of the copepod-invader, *Oithona davisae*, in the coastal waters of the Black Sea. *Rossiiskii zhurnal biologicheskikh invazii*, 2016, vol. 9, no. 3, pp. 90–100. (in Russ.)
15. Temnykh A. V., Zagorodnyaya Yu. A., Moryakova V. K. Spatial variability of seasonal dynamics of zooplankton in coastal waters of southwestern Crimea in 2002 and 2003. *Ekologiya morya*, 2008, iss. 75, pp. 23–30. (in Russ.). https://repository.marine-research.ru/handle/299011/4795
16. Clarke K. R., Warwick R. M. *Change*

in Marine Communities: An Approach to Statistical Analysis and Interpretation. 2nd ed. Plymouth : PRIMER-E Ltd., 2001, 171 p.
17. Gubanova A. D., Polikarpov I. G., Saburova M. A., Prusova I. Yu. Long-term dynamics of mesozooplankton by the example of the Copepoda community in Sevastopol Bay (1976–1996). *Oceanology*, 2002, vol. 42, no. 4, pp. 512–520.
18. Gubanova A. D., Garbazey O. A., Popova E. V., Altukhov D. A., Mukhanov V. S. *Oithona davisae*: Naturalization in the Black Sea, interannual and seasonal dynamics, and effect on the structure of the planktonic copepod community. *Oceanology*, 2019, vol. 59, no. 6, pp. 912–919. https://doi.org/10.1134/S0001437019060079
19. Gubanova A., Drapun I., Garbazey O., Krivenko O., Vodiasova E. *Pseudodiaptomus marinus* Sato, 1913 in the Black Sea: Morphology, genetic analysis, and variability in seasonal and interannual abundance. *PeerJ*, 2020, vol. 8, art. no. e10153 (26 p.). https://doi.org/10.7717/peerj.10153

ПРОСТРАНСТВЕННО-ВРЕМЕННАЯ ДИНАМИКА СТРУКТУРЫ СООБЩЕСТВА ЗООПЛАНКТОНА В ПРИБРЕЖНЫХ ВОДАХ У СЕВАСТОПОЛЯ В ВЕСЕННЕ-ОСЕННИЙ ПЕРИОД

Е. А. Галаговец, И. Ю. Прусова

ФГБУН ФИЦ «Институт биологии южных морей имени А. О. Ковалевского РАН», Севастополь, Российская Федерация

E-mail: *didobe@mail.ru*

Зоопланктон прибрежной зоны у Севастополя изучен довольно хорошо, однако комплексных работ с характеристикой всех таксонов, формирующих зоопланктонные сообщества данного региона, немного. Кроме того, проведённые ранее исследования в основном базировались на материалах, собранных в Севастопольской бухте на одной или двух станциях (у входа и/или в кутовой части), при этом анализ пространственной изменчивости зоопланктона внутри акватории бухты выполнен не был. Цель настоящей работы — охарактеризовать пространственно-временну́ю динамику сообществ зоопланктона Севастопольской бухты и прилегающих открытых вод в весенне-осенний период 2013 г. Материалом послужили пробы зоопланктона, собранные с апреля по ноябрь 2013 г. в западной, центральной и восточной частях Севастопольской бухты, а также на трёх станциях в открытом прибрежье — в двух милях от входа в бухту, возле посёлка Учкуевка и у входа в бухту Круглая. Оценку пространственно-временны́х различий таксономической структуры сообществ зоопланктона проводили с использованием процедур анализа сходства (ANOSIM), непараметрического многомерного шкалирования (MDS) и определения вклада отдельных таксонов в сходство/различие Брея — Кёртиса между группами проб (SIMPER). При анализе бета-разнообразия применяли индекс Шеннона. Исследование показало, что в рассматриваемый период между разными частями акватории Севастопольской бухты и прилегающего открытого прибрежья имелись пространственно-временны́е различия в количественных показателях и таксономической структуре зоопланктонных сообществ. Наибольший уровень различий в таксономической структуре зоопланктона отмечен между центрально-восточной частью бухты и открытым прибрежьем. При сравнении сообществ этих акваторий значения тестовой статистики *R* (ANOSIM) весной, летом и осенью составили 0,926; 0,572 и 0,761 (p < 0,03) соответственно. Средняя численность суммарного зоопланктона во все сезоны в бухте была выше, чем в открытом прибрежье, — (5,3 ± 1,9), (16,3 ± 2,7) и (8,3 ± 1,4) тыс. экз.·м$^{-3}$ против (0,8 ± 0,3), (4,6 ± 1,2) и (3,4 ± 1,3) тыс. экз.·м$^{-3}$ весной, летом и осенью соответственно (среднее ± *SE*; p < 0,006). Отмечена тенденция к более высоким величинам плотности в срединной части бухты. Выявлено изменение уровня разнообразия и, соответственно, степени сложности сообщества зоопланктона в пространственно-временно́м аспекте. Наиболее низкий уровень разнообразия зарегистрирован весной при средней (± *SE*) величине индекса Шеннона *H'* 1,09 ± 0,16; летом и осенью значения возросли до 1,94 ± 0,11 и 1,48 ± 0,09 соответственно. В летне-осенний период вели́чины *H'* были выше в зоне открытого прибрежья (2,07 ± 0,09) и ниже в акватории внутри бухты (1,53 ± 0,09). Определено, что различия в таксономической структуре между сообществами сравниваемых акваторий весной обусловлены тремя, летом — девятью, осенью — пятью доминирующими таксонами.

Ключевые слова: зоопланктон, копеподы, таксономическая структура, разнообразие, Севастопольская бухта